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Multidecadal otolith growth histories for red and gray snapper (*Lutjanus spp.*) in the northern Gulf of Mexico, USA

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ABSTRACT

Dendrochronology (tree-ring analysis) techniques were applied to develop chronologies from the annual growth-increment widths of red snapper (*Lutjanus campechanus*) and gray snapper (*Lutjanus griseus*) otoliths sampled from the northern Gulf of Mexico, USA. Growth increment widths showed considerable synchrony within and across species, indicating that some component of environmental variability influenced growth. The final, exactly dated red snapper chronology continuously spanned 1975 through 2003, while the gray snapper chronology continuously spanned 1975 through 2006. To determine baseline climate-growth relationships, chronologies were compared to monthly averages of sea surface temperatures, U winds (west to east), V winds (south to north), and Mississippi River discharge. The gray snapper chronology significantly ($P < 0.01$) correlated with winds and temperature in March and April, while the red snapper chronology correlated with winds in March. Principal components regression including springtime winds and temperature accounted for 28 and 52% of the variance in the red and gray snapper chronologies, respectively. These results indicate that snapper growth was favored by warm sea surface temperatures and onshore winds from the southeast to the northwest in March and April. Overall, this study provides preliminary, baseline information regarding the association between climate and growth for these commercially important snapper species.

Key words: climate, dendrochronology, gray snapper, Gulf of Mexico, otolith, red snapper, sclerochronology

INTRODUCTION

For more than a century, red snapper (*Lutjanus campechanus*) has supported a fishery in the northern Gulf of Mexico and today it remains one of the most economically and ecologically important species in the region (Collins, 1887; Goodyear, 1995). However, this history of heavy exploitation has significantly reduced populations, as evidenced from a decline in recreational landings from a high of 4.2 million pounds in 1980 to 1.4 million pounds by 1990 (Schirripa and Legault, 1999). Since its first assessment in 1988, red snapper has been classified as over-fished, and this has led to a series of controversial management measures intended to rebuild the stock, which only recently has shown signs of recovery (Hood *et al.*, 2007; Cowan *et al.*, 2010).

As a consequence of recent catch restrictions on red snapper, fishing pressure may be increasing on other species, particularly gray snapper (*Lutjanus griseus*) (Fischer *et al.*, 2005). This species overlaps in distribution with red snapper in the northern Gulf of Mexico and shares a preference for reefs and other hard-bottom substrates (Hoese and Moore, 1977). Gray snapper now supports a large recreational fishery in the Gulf of Mexico that landed over 1.6 million pounds in 2009, in addition to a smaller commercial fishery that landed over 248 000 pounds the same year (National Marine Fisheries Statistics Division, Silver Spring, MD, personal communication). Maximum ages for red and gray snapper as validated through bomb radio carbon (^{14}C) are 58 and 28 yr, respectively, both sufficiently long to be particularly vulnerable to overfishing (Baker and Wilson, 2001; Fischer *et al.*, 2005). Due to increasing exploitation, the Gulf of Mexico Reef Fish Stock Assessment Panel has recommended that gray snapper be considered for future stock assessment (RFSAP, 1999).

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As interest in these snapper species increases, more baseline information is required with respect to long-term growth patterns and their relationships to climate variability. Such information would help identify the climate variables to which the two snapper species are most sensitive, and would also facilitate the disentanglement of human and environmental factors on fish growth. Moreover, red and gray snapper are upper-level predators, and their growth could reflect lower-trophic processes that are themselves environmentally driven.

One way to address these issues in marine systems is the application of tree-ring (dendrochronology) techniques to develop multidecadal, exactly dated chronologies of fish growth from otolith increment widths. Resulting otolith chronologies are of a quality comparable to that in tree-ring chronologies and have been used to assess long-term trends and impacts of climate on fish growth (Black *et al.*, 2005, 2008a). For example, a splitnose rockfish (*Sebastes diploproa*) and yelloweye rockfish (*Sebastes ruberrimus*) chronology in combination with records of seabird reproductive success corroborate the importance of wintertime ocean conditions to the functioning of the California Current Ecosystem of the northeast Pacific (Black *et al.*, 2010). Moreover, these results suggest that environmental variability is driving lower-trophic productivity, which in turn regulates growth and reproduction. Farther north in the eastern Bering Sea, northern rock sole (*Lepidopsetta polyxystra*), yellowfin sole (*Limanda aspera*), and Alaska plaice (*Pleuronectes quadrituberculatus*) chronologies strongly relate to one another as well as instrumental records of spring and summer bottom temperatures, underscoring the importance of warm ocean conditions to growth in these species (Matta *et al.*, 2010).

Red and gray snapper are sufficiently long-lived that dendrochronology techniques could be used to establish multidecadal time series of otolith growth and address analogous issues in the northern Gulf of Mexico. Chronologies may yield valuable ecological information relevant to these economically important snapper species, and in a system for which relatively few long-term biological time series exist. Perhaps most fundamental is to determine whether synchronous growth is evident within or among these subtropical species, indicating at least some influence from environmental variability. Thus, the first goal of this study is to evaluate the extent to which growth patterns are shared among individuals within each species. If synchrony is strong, subsequent goals are to implement tree-ring techniques to develop otolith growth-increment chronologies, and quantify the level of synchrony between the two species. Finally, few studies have attempted to link environmental variability and productivity in the Gulf of Mexico region, especially over multi-year timescales. Thus, the last goal of the study is to explore baseline relationships between snapper growth-increment chronologies and ocean climate in the northern Gulf of Mexico.

MATERIALS AND METHODS

The red and gray snapper used in this study were sampled between 1991 and 2007 from recreational, commercial, and fishery-independent landings from Louisiana and Florida (Fig. 1). Sagittal otoliths were thin-sectioned through the transverse plane with a high-speed saw to a thickness of 0.5 mm following the methods of Cowan *et al.* (1995). Otoliths aged via annulus counts to be at least 20 yr old for red snapper and 15 yr old for gray snapper were retained. Of this limited set, only those otoliths in which growth-increment boundaries were well defined and easily discerned were ultimately chosen for chronology development. This represented approximately half of the sufficiently old snapper otoliths and approximately 80% of the sufficiently old gray snapper otoliths. For both red and gray snapper, growth increments were analyzed along the dorsal side of the sulcal groove (Fig. 2). Red snapper otoliths were observed with reflected light and gray snapper otoliths with transmitted light. All samples were viewed with a binocular dissecting microscope at 40× magnification.

In the first step of chronology development, visual crossdating was applied to ensure the exact dating of all growth increments. This procedure, borrowed from dendrochronology, is based on the principle that at least one climatic variable limits growth and fluctuates over time, inducing synchronous growth patterns among individuals of a given species and region. These synchronous growth patterns, much like bar codes, can then be cross-matched among individuals to verify that all growth increments have been correctly identified and assigned the correct calendar year of formation (Fritts, 1976; Yamaguchi, 1991).

Cross-dating was conducted separately in each species, always beginning at the marginal growth increment known to have formed at the calendar year of capture. From this dated increment, synchronous growth patterns were used to verify dates of successively earlier increments, ending with the innermost increment (Black *et al.*, 2005). Had an error been made and an increment missed or falsely added, the growth pattern in that individual would

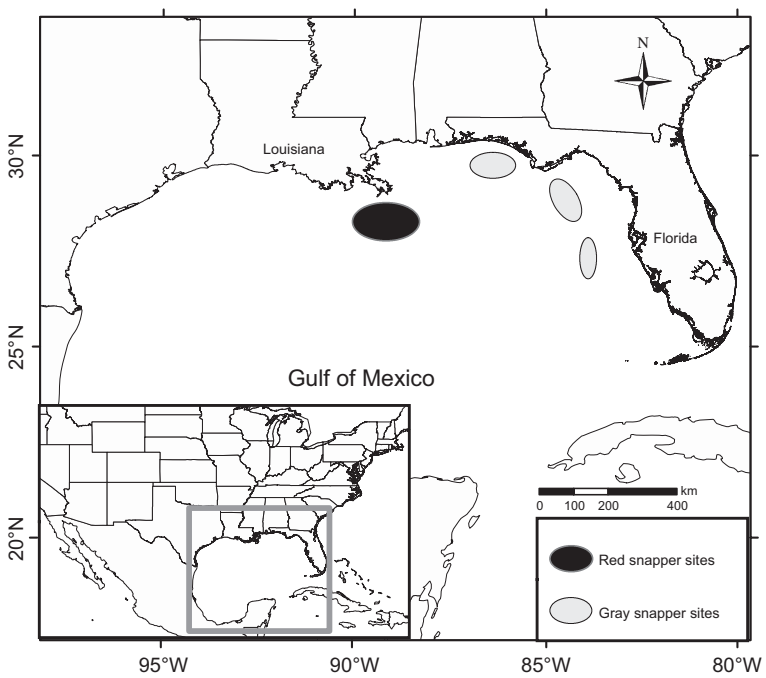


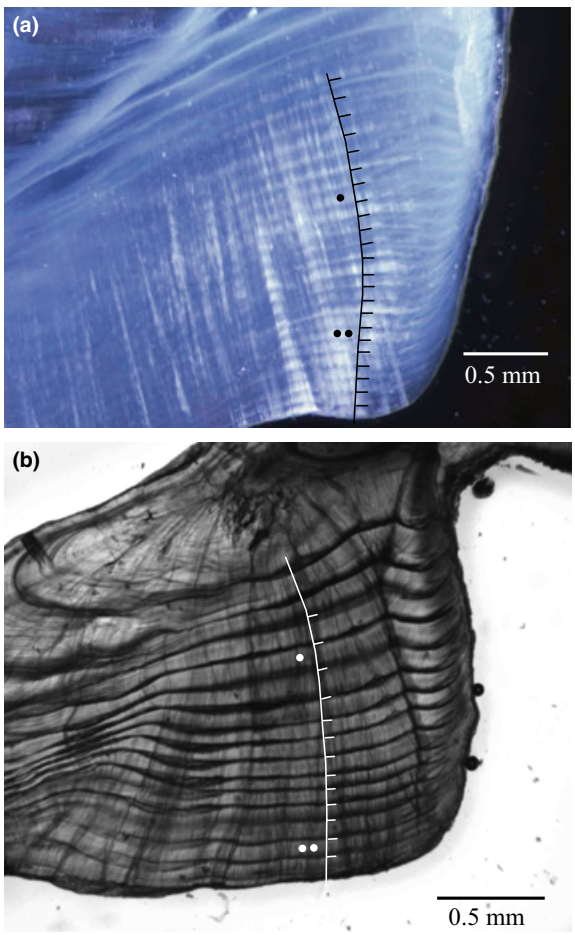
Figure 1. Map of the northern Gulf of Mexico study area with the collection areas for red snapper and gray snapper individuals used in chronology development.

have been misaligned by a year, beginning at the point where the error occurred. When all growth increments were correctly identified, growth patterns aligned. At no time, however, were these growth patterns 'forced' on samples. If the pattern in an individual was offset, a correction was made only if a true growth-increment boundary was evident upon re-inspection. Given the high otolith clarity, errors were uncommon and almost all could be attributed to misinterpretations at the otolith margin. Ultimately, all otoliths crossdated and none were discarded due to asynchronous growth.

Once visual crossdating was complete, all samples were photographed with a Leica DC300 3.0 megapixel digital camera and the growth increment widths measured using the program IMAGEPRO PLUS v.6.0 (Media Cybernetics, Silver Spring, MD, USA). Growth increments were measured continuously from the dorsal distal margin to within 3 yr of the focus, or as close to the focus as possible. One complete increment was defined as the distance from the distal side of the previous year's opaque zone to the distal side of the current year's opaque zone, noting that opaque zones appeared white under reflected light and dark under transmitted light. The first 3 yr of growth were excluded due to the rapidly changing geometry of the otolith and to avoid the juvenile life stages. In total, two axes were measured per otolith, always following the direction of growth (i.e. perpendicular to the growth increments) (Fig. 2).

Crossdating was statistically verified within each species using the International Tree-Ring Data Bank Program Library program COFECHA, available through the University of Arizona Laboratory of Tree-Ring Research http://www.ltrr.arizona.edu/pub/dpl/ (Grissino-Mayer, 2001). To date, this program has been used to verify crossdating in a variety of marine fish and bivalve species (Black *et al*., 2008a,b). First, COFECHA was used to fit each set of otolith measurements with a highly flexible cubic spline set at a 50% frequency response of 22 yr (Grissino-Mayer, 2001). Ring width measurements were then divided by the values predicted by the spline function, removing low-frequency variability and standardizing all measurement time series to a mean of one. Any remaining autocorrelation was removed via autoregressive modeling in COFECHA to ensure that all detrended time series met the assumptions of serial independence. Each standardized time series was then correlated with the average of all other standardized measurement time series in the sample set, the mean of which was reported as the interseries correlation. Isolating only the high frequency, serially independent growth pattern prevented spuriously high correlations among measurement time series and also mathematically mimicked the process of visual crossdating. Ultimately, this analysis provided a statistical screening tool, yet all final decisions about crossdating were made by visual inspection of the sample. Also calculated in COFECHA was mean sensitivity, a measure of

Figure 2. Photographs of the dorsal half of otolith thin-sections for (a) red snapper using reflected light and (b) gray snapper using transmitted light. The axis of measurement is shown as are growth-increment boundaries. The year 1990 is labeled as a single dot and the year 2000 is labeled as a double dot.



high-frequency variability among pairs of successive increments, which ranges from a minimum of zero (a pair of increments of the same width) to a maximum of two (a pair of increments in which one value is zero) (Fritts, 1976).

Once crossdating verification was complete, the red and gray snapper master chronologies could be developed. In the first step of building the chronologies, we detrended each original measurement time series with a negative exponential function. Negative exponential functions removed age-related growth declines while preserving as much remaining low-frequency variability as possible. Note that this detrending process contrasted with the highly flexible cubic splines used in the separate process of crossdating verification. Within each species, all measurement time series detrended with negative exponential functions were then averaged into a master chronology using a biweight robust mean to reduce the effect of outliers (Cook, 1985). All chronology development was conducted using the program ARSTAN (developed by Ed Cook and Paul Krusic; available at http://www.ldeo.columbia.edu/res/fac/trl/public/publicSoftware.html) (Cook, 1985).

Given the lack of information regarding environmental forcing on productivity or growth in the northern Gulf of Mexico, particularly on multidecadal timescales, we could not develop specific hypotheses concerning the relationships between the growth-increment chronologies and climate. To limit the number of variables, the analysis was restricted to records that spanned the majority of each chronology and represented the most likely climate drivers for the region. Winds were chosen given their influence on currents, as was Mississippi River discharge given its potential as a major source of nutrient input. Sea surface temperatures (SST) were also included as an additional indicator of ocean circulation, especially with respect to the Loop Current. Each snapper master chronology was related to monthly averages of climate variables as a way to determine those periods of the year during which environmental variability most strongly affected growth.

Hadley HadISST 1.1 1-degree gridded SST data were obtained from http://badc.nerc.ac.uk/data/hadisst/. Wind data were obtained from the North American Regional Reanalysis http://www.emc.ncep.noaa.gov/mmb/rreanl/, available in a $0.375 \times 0.375°$ grid. SST data spanned the full length of the chronologies, although winds were limited to 1979. U winds (west to east), and V winds (south to north) were averaged between 28 and 30°N latitude, and from −83 to −90°W longitude, the approximate sampling locations of the fish used to develop the chronology. Monthly averages of Mississippi River discharge at Talbert Landing, Mississippi (gage ID 01100) were obtained through the US Army Corps of Engineers at http://www.mvn.usace.army.mil/cgi-bin/wcmanual.pl?01100 and spanned the full length of both chronologies. Each snapper chronology was correlated with the monthly averages of these four climate variables over the current year as well as the prior year to detect any lagged relationships. Thus, 96 variables were considered; 24 each for U winds, V winds, SST, and Mississipi River discharge. Only highly significant ($P < 0.01$) correlations were retained. Considering that significant correlations often occurred among climate variables, principal components regression was used to better define

climate–growth relationships. As a final summary analysis, mean temperature and wind fields were calculated for the four calendar years with the highest chronology values and the four calendar years with the lowest chronology values. The analysis was repeated for the red and the gray snapper.

RESULTS

Gray snapper otoliths were available along much of the Florida coast, although otolith clarity substantially diminished south of approximately 28°N, restricting chronology development to higher latitudes. The oldest red snapper individuals were concentrated off Louisiana, somewhat farther to the west (Fig. 1). Growth was strongly synchronous within and even between species, which facilitated crossdating. For example, conspicuously narrow increments tended to occur in 1996, 1993, 1987, and 1978, and conspicuously wide increments in 1999, 1990, 1982, and 1979. Age-related growth declines were present in both species (Fig. 3A,C); when these were removed via detrending with negative exponential functions, a high degree of growth synchrony was revealed among individuals (Fig. 3B,D). The final red and gray snapper chronologies were strongly and positively related to one another with an R^2 of 0.45; $P < 0.001$ in a linear regression (data not shown). Interseries correlation and mean sensitivity were, however, somewhat higher for gray snapper, suggesting a greater degree of synchrony among gray snapper individuals and a greater degree of year-to-year variability in growth (Table 1). The red snapper chronology contained highly significant first-order autocorrelation ($R = -0.62$; $P = 0.0004$) but the gray snapper did not ($R = -0.30$; $P = 0.105$). Prior to correlating the red snapper chronology to climate variables, autocorrelation was removed via autoregressive modeling in the program ARSTAN. Use of the red snapper chronology in which autocorrelation had been removed helped to prevent spurious climate–growth relationships.

The gray snapper chronology was significantly ($P < 0.01$) correlated with March SST, U winds, and V winds as well as April SST. The red snapper chronology was also correlated with March U winds in addition to V winds during the prior June (Table 2). In both species, chronologies were positively related to SST and V winds, but negatively related to U winds. Thus, warm temperatures, winds from the south to the north, and winds from the east to the west (i.e., winds from the southeast to the northwest) were favorably associated with growth, especially in March and April. Mississippi River discharge was not significantly correlated with either chronology at the $P < 0.01$ level or

Figure 3. Ring-width measurements for (a) red snapper and (c) gray snapper. Measurement time series for (b) red snapper and (d) gray snapper after detrending with negative exponential functions. Black line is the mean.

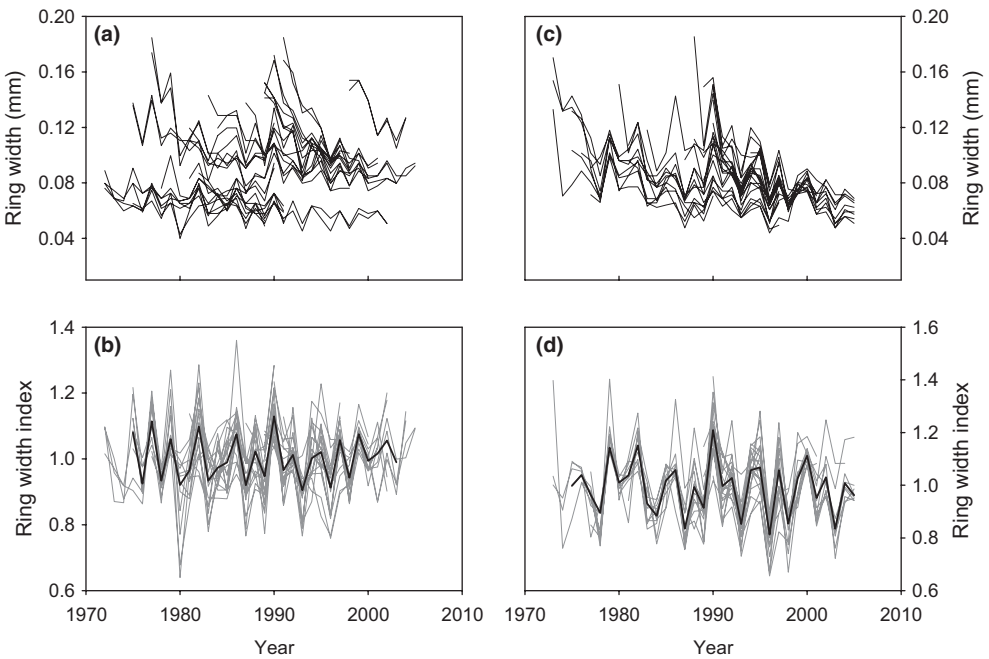


Table 1. Red and gray snapper chronology properties.

Chronology	Sample size[†]	Mean sensitivity[‡]	Interseries correlation[§]	Mean series length (yr)
Red snapper	30	0.13	0.54	15.4
Gray snapper	24	0.18	0.76	17.1

[†]The number of measurement time series used in developing each chronology.
[‡]An index of high-frequency variability that ranges from 0 (no variability) to 1 (high variability).
[§]The average correlation between each detrended measurement time series and the average of all other detrended measurement time series as calculated by COFECHA.

Table 2. Significant ($P < 0.01$) correlations (Pearson; R) between the red and gray otolith chronologies and monthly averaged climate variables. Climate variables include U winds (west to east), and V winds (south to north), and sea surface temperatures (SST). Monthly means for each variable were considered for the current years as well as the prior (pr) year.

Variable	R	P
Red snapper		
March U winds	−0.48	0.01
prJune V winds	0.52	0.008
Gray snapper		
March U winds	−0.53	0.003
March V winds	0.56	0.002
March SST	0.55	0.001
April SST	0.57	<0.001

even the $P < 0.05$ level, and was dropped from further analysis.

Winds and SST were all significantly ($P < 0.05$) correlated with one another during March and April (data not shown). To avoid problems with collinearity and to best capture overall ocean conditions with respect to winds and temperature, principal components regression (PCR) was used to better relate climate to the snapper chronologies. For the red snapper analysis, March SST, U winds, and V winds were first entered into principal components analysis, and the leading component captured 60% of the variability in these three climate variables (eigenvalue = 1.8). The second component captured only 21% of the variability in the climate data (eigenvalue = 0.65) and was dropped from further analysis. A multiple stepwise regression ($P < 0.01$ to enter) was performed for red snapper in which this leading March principal component was entered as well as prior June V winds. Only the March principal component was significant ($P = 0.0066$) and explained 23% of the variance in the chronology. The Durbin–Watson statistic (DW) was calculated as a check for autocorrelation in the regression residuals, but was not significant (DW = 2.06 and $P = 0.60$) (Fig. 4A).

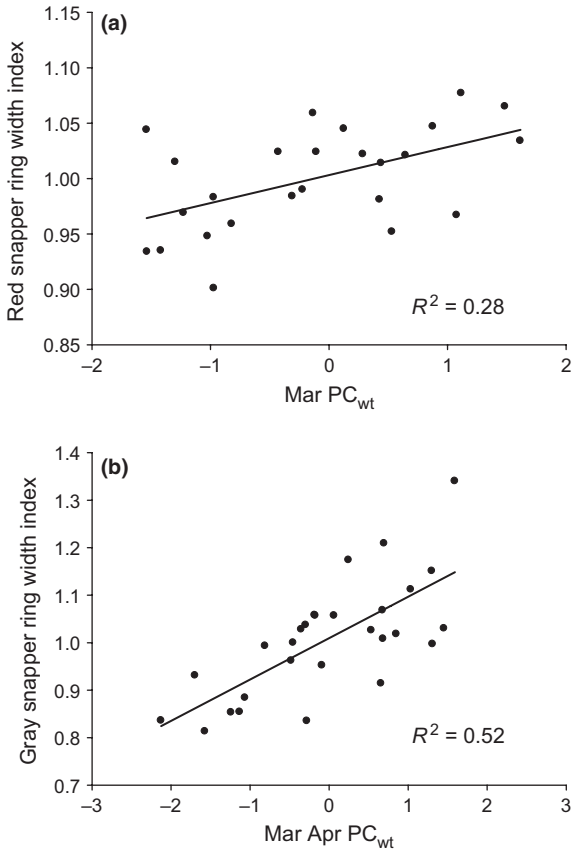
For the gray snapper analysis, SST, U winds, and V winds for March and April were entered into principal components analysis. The leading principal component captured 42% of the variability from these six climate variables (eigenvalue = 2.5) ($R^2 = 0.56$; $P < 0.0001$) and the second component captured an additional 25% (eigenvalue = 1.5). All other components captured less than 12% of the variance in the data set and were dropped from further analysis. The first two principal components for March and April climate were entered into a stepwise regression ($P < 0.01$ to enter) against the gray snapper chronology but only the leading principal component was significant ($R^2 = 0.56$ $P < 0.0001$; DW = 1.98; $P = 0.49$) (Fig. 4B). For both the red snapper and gray snapper analyses, the leading principal components for climate were positively associated with SST, positively related to V winds, and negatively related to U winds. Thus, the positive relationships between principal components and the snapper chronologies indicated that warm SST, winds from the south to the north, and winds from the east to the west (i.e., winds from the southeast to the northwest) were favorable for growth (Fig. 4).

As a final analysis, March SST and wind fields were averaged in the lowest four (1996, 2003, 1987, 1993; Fig. 5A) and highest four (2000, 1982, 1979, 1990; Fig. 5B) years of growth in gray snapper and then for the lowest four (1993, 1996, 1987, 1980; Fig. 5C) and highest four (1986, 1999, 1982, 1990; Fig. 5D) years of growth in red snapper. Good years for red snapper or gray snapper growth were characterized by SST approximately 1°C warmer than poor years in addition to winds being predominantly from the southeast to the northwest as opposed to from the northeast to the southwest (Fig. 5).

DISCUSSION

High interseries correlations indicated that growth patterns were strongly synchronous within each species. Values were comparable to those described for other marine fish and bivalve growth-increment data sets, such as Pacific geoduck (0.69–0.75) and Pacific rockfish (~0.55) along the coast of western North America (Black, 2009). Indeed, series intercorrelations between 0.55 and 0.75 have commonly been

Figure 4. (a) Relationship between the red snapper otolith growth-increment chronology and the leading principal component of March sea surface temperatures, U winds, and V winds (Mar PC_{wt}). (b) Relationship between the gray snapper otolith growth-increment chronology and the leading principal component of March and April sea surface temperatures, U winds, and V winds (Mar Apr PC_{wt}).

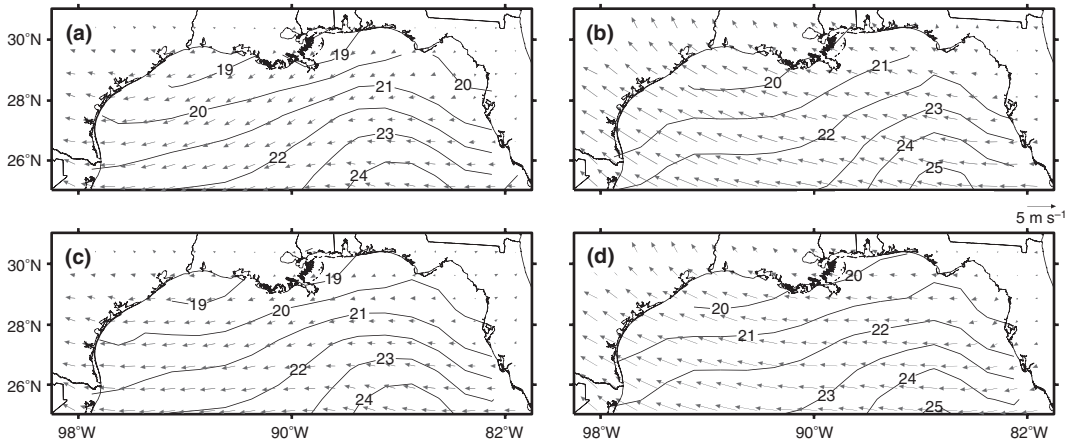


identified in dendrochronology (tree-ring) studies. Interseries correlations values were, however, greater in gray snapper, likely due to superior otolith clarity. For the gray snapper otoliths used in this study, growth increments were prominently defined with boundaries that could be consistently and accurately demarcated. Yet it should be noted that this was not the case for gray snapper otoliths everywhere in the eastern Gulf of Mexico. Otolith clarity followed a strong latitudinal gradient such that growth-increment boundaries became increasingly diffuse to the south, particularly below 28°N latitude. In an analysis of *Stegastes planifrons* and *Stegastes partitus* in the western Atlantic and Gulf of Mexico, Caldow and Wellington (2003) found that otolith clarity was greatest in sites that experienced the widest range of intra-annual water temperatures. Thus, trends in gray snapper clarity may reflect the transition along the west Florida coast from a temperate to a more stable semi-tropical climate (Zieman and Zieman, 1989). Ultimately, growth-increment contrast for gray snapper was so poor south of 28°N that samples could not be used for chronology development.

In contrast to the gray snapper otoliths used in this study, red snapper otoliths were more opaque and had relatively diffuse growth-increment boundaries. This could simply be due to species-specific differences in otolith structure and chemistry. Another contributing factor may be that the red snapper sampled for this study were collected at greater depths (31–146 m, mean 73.2 m) than the gray snapper (10–87 m, mean 43.8 m). If environmental variability was less pronounced in these somewhat deeper waters, the absence of strong seasonal transitions could reduce otolith growth-increment clarity. On interannual timescales, variability in otolith growth-increment widths would be muted. Whether a matter of otolith structure, habitat or some other variable, red snapper growth-increment boundaries were comparatively unclear, were more difficult to measure, and showed lower levels of interannual variability, all contributing to lower mean sensitivities, lower interseries correlations, and weaker relationships to climate variables.

Despite these differences in otolith clarity, depth, and the spatial extents involved, growth patterns across species were remarkably consistent. Red and gray snapper do share similar life histories; both are considered to be generalized, opportunistic carnivores (Starck, 1971; Parrish, 1987; McCawley and Cowan., 2007) that as adults occupy similar natural and artificial reef habitat in the northern Gulf of Mexico (Fischer *et al.*, 2004, 2005). Such a high degree of synchrony in these two related species suggestsed that growth was affected by broad-scale patterns in environmental variability that spanned the study region. Notably, both chronologies were dominated by higher-frequency variability and lacked multi-year trends that might indicate long-term changes in competitive status of these species. However, the ability to resolve multidecadal growth trends was limited by detrending. The process of removing ontogenetic growth declines also removed any trends longer than the given measurement time series in a phenomenon known to dendrochronology as the 'segment length curse' (Cook *et al.*, 1995). Thus, trends that exceed approximately 15 yr, the mean length of the measurement time series used to construct each chronology, would have been eliminated. Combining a greater range of historically collected specimens with a detrending techniques known as regional curve standardization could better

Figure 5. Mean March wind vectors and sea surface temperatures for (a) the four lowest calendar years of the gray snapper chronology, (b) the four highest calendar years of the gray snapper chronology, (c) the four lowest calendar years of the red snapper chronology, and (d) the four highest calendar years of the red snapper chronology. Wind vectors are shown as arrows, the lengths of which indicate wind speed. Contours of mean temperature are also shown and labeled in degrees Celsius.



preserve low-frequency variability (Esper *et al.*, 2002). However, this data set provided valuable information on decadal to sub-decadal processed over the past 30 yr, and indicated that no dramatic or sudden changes in growth rate have occurred over these timescales.

In comparison with instrumental environmental records, both species showed strong seasonality in their responses to climate with peak sensitivities in March and April. Favorable growth for snapper appears to be associated with warm water temperatures and winds from the southeast during these spring months. However, the mechanisms underlying the linkage between snapper growth and this pattern of temperature and winds are unclear. One possibility is that warm temperatures directly enhance growth by increasing fish metabolic rates. Alternatively, climate patterns could indirectly influence snapper growth via linkages to lower trophic productivity in the northeastern Gulf of Mexico. For example rockfish (*Sebastes* spp.) otolith chronologies in the California Current Ecosystem positively relate to upwelling intensity while negatively relating to temperature, suggesting indirect linkages between climate and growth via upwelling-driven productivity (Black, 2009; Thompson and Hannah, 2010).

The fact that spring months were most closely related to snapper otolith growth suggested that the timing of seasonal transitions was important, and with possible implications for the transport of nutrient-rich freshwater into the study region. In the northeastern Gulf of Mexico, wind stress and surface currents occur in distinct summer and winter patterns. During the winter and fall, winds tend to be northeasterly, transitioning to the southeast in the summer months as the Bermuda High strengthens off the eastern United States seaboard (Morey *et al.*, 2003a; Johnson, 2008). An early change to the summer pattern could warm waters and stimulate fish metabolism, although such a shift could also influence lower-trophic productivity. During the summer, Ekman transport associated with winds from the south would move surface waters to the east, including discharges from the nutrient-rich Mississippi and neighboring Atchafalaya Rivers (Morey *et al.*, 2003a,b). These freshwater inputs could be further distributed as they become entrained by mesoscale eddies that periodically move through the region, providing a nutrient source in offshore waters (Morey *et al.*, 2003b).

Previous studies in the eastern Gulf of Mexico have documented low-salinity, high chlorophyll-content plumes likely associated with river discharge (Paul *et al.*, 2000; Del Castillo *et al.*, 2001). If in fact this infusion of low-salinity, nutrient-rich waters boosts productivity, it could account for relationships between snapper chronologies and winds. Indeed, the summer pattern of wind stress is strikingly similar to that observed during favorable growth years, while the non-summer pattern of wind stress reflects that observed during poor years of snapper growth (Fig. 5) (Johnson, 2008). Such a mechanism could also account for the lack of correlation between snapper chronologies and Mississippi River discharge in that river volume would be much less important than the transport of the discharged water to the eastern Gulf of Mexico (Morey *et al.*, 2003b). The river may experience high flow events, but the water must be moved to the study region for it to impact productivity. This

would be particularly relevant for red snapper, which were collected relatively close to the Mississippi River Delta. Farther east, Apalachicola River discharge and episodic wind-driven transport have been linked to plumes of chlorophyll over the northern West Florida Shelf, especially between January and March (Morey *et al.*, 2009). Yet, as with the Mississippi River, the gray and red snapper chronologies do not significantly ($P < 0.01$) correlate with monthly-averaged Apalachicola River discharge (USGS station 2358000 at Chattahoochee, FL; data not shown). This further suggests that if freshwater inputs are important to red and gray snapper growth, they must be distributed by the appropriate winds and currents.

Beyond winds, the Loop Current is another influential driver of circulation in the eastern Gulf of Mexico. Currents moving along the western boundary of the Atlantic Basin flow through the Yucatan Channel and extend northward into the Gulf of Mexico before exiting through the Straits of Florida between Cuba and the Florida Keys. The distance at which the Loop Current extends into the Gulf of Mexico varies considerably, and northerly protrusions can separate to form Loop Current Eddies that drift to the west and slowly dissipate. These eddies are typically 200–400 km in diameter and can greatly affect circulation and productivity throughout the water column via upwelling, water mixing, and broad-scale transport of water masses, nutrients, dissolved oxygen, and organic material (Elliott, 1982; Morey *et al.*, 2003a; Jochens and DiMarco, 2008). Though the Loop Current and associated eddies are apparent in sea surface height fields (Jochens and DiMarco, 2008), altimeter data are of insufficient length for the purposes of this study. Sea surface temperatures may capture some Loop Current dynamics, but only very coarsely and with considerable influence from other atmospheric processes. If they could be developed, multidecadal indices of Loop Current dynamics may account for additional variance in the red and gray snapper chronologies.

Overall, our results indicate that winds and temperatures during March and April are related to red and gray snapper growth, although the mechanisms are unclear. Such strong correlations during these spring months could reflect the importance of the timing of the transition between a wintertime climate pattern and a summertime climate pattern. If the summer pattern is conducive to faster growth via warmer temperatures or climatic conditions that favor lower-trophic productivity, then an early shift from winter could lengthen the growing season, resulting in a wider growth increment. Ultimately, comparisons between snapper chronologies and lower-trophic productivity indices such as chlorophyll may prove helpful in identifying whether climate exerts direct or indirect influences on snapper growth. However, this will require future updates of red and gray snapper chronologies to increase overlap with remote-sensed data such as SeaWiFS, which at present share only 7 yr with the red snapper chronology.

In conclusion, our findings must be interpreted with caution; these chronologies represent only one aspect of snapper ecology, and if analogous to those in Pacific rockfish, are most likely associated with overall body condition and fat reserves (Black, 2009). The chronologies do not necessarily reflect the number of fish in the population or total population biomass, nor recruitment or reproductive success. When combined with other indices specific to snapper, or possibly growth-increment chronologies from species of contrasting life histories, they may provide additional insight into ecosystem function and corroborate the importance of springtime ocean conditions. Moreover, the climate variables are limited and probably do not include the considerable influences of the Loop Current in the northeastern Gulf of Mexico. The chronologies do, however, provide unique, multidecadal perspectives on red and gray snapper growth and provide preliminary, baseline information concerning the importance of winter and springtime ocean conditions to growth in these species.

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REFERENCES

Baker, M.S. and Wilson, C.A. (2001) Use of bomb radiocarbon to validate otolith section ages of red snapper *Lutjanus campechanus* from the northern Gulf of Mexico. *Limnol. Oceanogr.* **46:**1819–1824.

Black, B.A. (2009) Climate driven synchrony across tree, bivalve, and rockfish growth-increment chronologies of the northeast Pacific. *Mar. Ecol. Prog. Ser.* **378:**37–46.

Black, B.A., Boehlert, G.W. and Yoklavich, M.M. (2005) Using tree-ring crossdating techniques to validate annual growth increments in long-lived fishes. *Can. J. Fish. Aquat. Sci.* **62:**2277–2284.

Black, B.A., Boehlert, G.W. and Yoklavich, M.M. (2008a) A tree-ring approach to establishing climate-growth

relationships for yelloweye rockfish in the northeast Pacific. *Fish. Oceanogr.* **17:**368–379.

Black, B.A., Gillespie, D., MacLellan, S.E. and Hand, C.M. (2008b) Establishing highly accurate production-age data using the tree-ring technique of crossdating: a case study for Pacific geoduck (*Panopea abrupta*). *Can. J. Fish. Aquat. Sci.* **65:**2572–2578.

Black, B.A., Schroeder, I.D., Sydeman, W.J., Bograd, S.J. and Lawson, P.W. (2010) Winter ocean conditions synchronize rockfish growth and seabird reproduction in the central California current ecosystem. *Can. J. Fish. Aquat. Sci.* **67:**1149–1158.

Caldow, C. and Wellington, G.M. (2003) Patterns of annual increment formation in otoliths of pomacentrids in the tropical western Atlantic: implications for population age-structure examination. *Mar. Ecol. Prog. Ser.* **265:**185–195.

Collins, J.W. (1887) Notes of the red snapper fishery. *Bull. U.S. Fish Comm.* **6:**299–300.

Cook, E.R. (1985) A time-series analysis approach to tree-ring standardization. Ph.D. Thesis (Ph.D.), University of Arizona, 171 pp.

Cook, E.R., Briffa, K.R., Meko, D.M., Graybill, D.A. and Funkhouser, G. (1995) The segment length curse in long tree-ring chronology development for paleoclimatic studies. *Holocene* **5:**229–237.

Cowan, J.H. Jr, Shipp, R.L., Bailey, H.K. and Haywick, D.W. (1995) Procedure for rapid processing of large otoliths. *Trans. Am. Fish. Soc.* **124:**280–282.

Cowan, J.H. Jr, Grimes, C.B., Patterson, W.F. III *et al.* (2010) Red snapper management in the Gulf of Mexico: science- or faith based? *Rev. Fish Biol. Fish.* **20:** doi: 10.1007/s11160-010-9165-7.

Del Castillo, C.E., Coble, P.G., Conmy, R.N., Muller-Karger, F.E., Vanderbloemen, L. and Vargo, G.A. (2001) Multispectral *in situ* measurements of organic matter and chlorophyll fluorescence in seawater: documenting the intrusion of the Mississippi River plume in the West Florida Shelf. *Limnol. Oceanogr.* **46:**1836–1843.

Elliott, B.A. (1982) Anticyclonic rings in the Gulf of Mexico. *J. Phys. Oceanogr.* **12:**1292–1309.

Esper, J., Cook, E.R. and Schweingruber, F.H. (2002) Low-frequency signals in long tree-ring chronologies for reconstructing past temperature variability. *Science* **295:**2250–2253.

Fischer, A.J., Baker, M.S. and Wilson, C.A. (2004) Red snapper (*Lutjanus campechanus*) demographic structure in the Northern Gulf of Mexico based on spatial patterns in growth rates and morphometrics. *Fish. Bull.* **102:**593–603.

Fischer, A.J., Baker, M.S., Wilson, C.A. and Nieland, D.L. (2005) Age, growth, mortality, and radiometric age validation of gray snapper (*Lutjanus griseus*) from Louisiana. *Fish. Bull.* **103:**307–319.

Fritts, H.C. (1976) *Tree Rings and Climate*. London: Academic Press, 567 pp.

Goodyear, C.P. (1995) *Red Snapper in U.S. Waters of the Gulf of Mexico*. Miami: National Marine Fisheries Service, Southeast Fisheries Science Center, Miami Laboratory.

Grissino-Mayer, H.D. (2001) Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree Ring Res.* **57:**205–221.

Hoese, H.D. and Moore, R.H. (1977) *Fishes of the Gulf of Mexico, Texas, Louisiana, and Adjacent Waters*. College Station: Texas A&M University Press, 327 pp.

Hood, P.B., Strelcheck, A.J. and Steele, P. (2007) A history of red snapper management in the Gulf of Mexico. In: *Red Snapper Ecology and Fisheries in the U.S. Gulf of Mexico*. W.F. Patterson III, J.H. Cowan, G.R. Fitzhugh & D.L. Nieland (eds) Bethesda: American Fisheries Society, pp. 267–284.

Jochens, A.E. and DiMarco, S.F. (2008) Physical oceanographic conditions in the deepwater Gulf of Mexico in summer 2000–2002. *Deep Sea Res. II* **55:**2541–2554.

Johnson, D.R. (2008) *Ocean Surface Current Climatology in the Northern Gulf of Mexico*. Ocean Springs, MS: Gulf Coast Research Laboratory.

Matta, M.E., Black, B.A. and Wilderbuer, T.K. (2010) Climate-driven synchrony in otolith growth-increment chronologies for three Bering Sea flatfish species. *Mar. Ecol. Prog. Ser.* **413:**137–145.

McCawley, J.R. and Cowan., J.H. (2007) Seasonal and size specific diet and prey demands of red snapper on Alabama artificial reefs. In: *Red Snapper Ecology and Fisheries in the U.S. Gulf of Mexico*. W.F. Patterson III, J.H. Cowan, G.R. Fitzhugh & D.L. Nieland (eds) Bethesda: American Fisheries Society, Symposium 60, pp 77–101.

Morey, S.L., Martin, P.J., O'Brien, J.J., Wallcraft, A.A. and Zavala-Hidalgo, J. (2003a) Export pathways for river discharged fresh water in the northern Gulf of Mexico. *J. Geophys. Res. Oceans* **108:** doi: 10.1029/2002JC001674.

Morey, S.L., Schroeder, W.W., O'Brien, J.J. and Zavala-Hidalgo, J. (2003b) The annual cycle of riverine influence in the eastern Gulf of Mexico basin. *Geophys. Res. Lett.* **30:** doi: 10.1029/2003GLO17348.

Morey, S.L., Dukhovskoy, D.S. and Bourassa, M.A. (2009) Connectivity of the Apalachicola River flow variability and the physical and bio-optical oceanic properties of the northern West Florida Shelf. *Cont. Shelf Res.* **29:**1264–1275.

Parrish, J.D. (1987) The trophic biology of snappers and groupers. In: *Tropical Snapper and Groupers: Biology and Fisheries Management*. J.J. Polovina & S. Ralston (eds) Boulder, CO: Westview Press, Inc., pp. 405–463.

Paul, J.H., Alfreider, A., Kang, J.B. *et al.* (2000) Form IA rbcL transcripts associated with a low salinity/high chlorophyll plume ('Green River') in the eastern Gulf of Mexico. *Mar. Ecol. Prog. Ser.* **198:**1–8.

RFSAP (1999) *September 1999 Report of the Reef Fish Stock Assessment Panel*. Tampa, FL: Gulf of Mexico Fishery Management Council, 32 pp.

Schirripa, M.J. and Legault, C.M. (1999) *Status of the Red Snapper in U.S. Waters of the Gulf of Mexico: Updated Through 1998*. NOAA Southeast Fisheries Science Center Sustainable Fisheries Division Contribution SFD-99/00-75. NOAA Southeast Fisheries Science Center, Miami, FL. 44 pp.

Starck, W.A. (1971) Biology of the gray snapper, *Lutjanus griseus* (Linnaeus), in the Florida keys. In: *Investigations on the Gray Snapper, Lutjanus griseus*. W.A. Starck & R.E. Schroeder (eds) Coral Gables, FL: University of Miami Press, pp. 11–150.

Thompson, J.E. and Hannah, R.W. (2010) Using cross-dating techniques to validate ages of aurora rockfish (*Sebastes aurora*): estimates of age, growth and female maturity. *Environ. Biol. Fishes* **88:**377–388.

Yamaguchi, D.K. (1991) A simple method for cross-dating increment cores from living trees. *Can. J. For. Res.* **21:**414–416.

Zieman, J.C. and Zieman, R.T. (1989) The ecology of the seagrass meadows of the west coast of Florida: a community profile. *U.S. Fish Wildl. Serv. Biol. Rep.* **85:**155.